

MATERNAL GENETIC COMPOSITION OF EARLY MEDIEVAL (6TH-10TH CENTURY AD) POPULATIONS LIVED IN THE CIS- AND TRANS-URAL AND VOLGA-KAMA REGIONS

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Many scientific theories exist about the origin of Hungarians and their migration from Northern Central Asia to Europe in the 8th–9th centuries AD. Ethnic heterogeneity of the Hungarian Conquerors is attested by a number of historical and archaeological evidence due to their associated migration with other populations from the Ural region through the Middle-Volga region (and the Khazar Khaganate) until their arrival in the Carpathian Basin in 895 AD. The source region, direction, and chronology of the migration is still unclear and intensively studied by historians, archaeologists and linguists. In our studies, we approach these issues using archaeogenetic methodology. We investigate early medieval (6th–10th AD) populations from the regions of the Ural Mountains, the presumed migration route and the Carpathian Basin. The sites can be associated with each other and the Hungarian Conquerors as well. Remains of the first cultures (Kushnarenkovo and Karayakupovo) associated with Hungarian prehistory are from the Middle and Southern Urals. Investigating whole mitochondrial genomes, our first series came from the eastern (Uyelgi) and western (Bayanovo, Sukhoy Log, Bartim) side of the Middle-Southern Urals. As a continuation we included samples from the Volga-Kama region, with special attention to Bolshie Tigani site. We might get a better picture of the migration route and can map its stages and stopovers in a genetic context by extending our database with mitochondrial data from the presented series.

Keywords: ancient mitochondrial DNA, maternal lineages, population genetics, Hungarian prehistory, Cis-Ural region, Trans-Ural region, Volga-Kama region.

Introduction

Until recently, the research on early Hungarians has been carried out mainly within the framework of humanities, however traditional anthropological studies always had an impact on the interpretations based on historical-linguistic and archaeological methods. Applying research methods of archaeogenetics can also make a great contribution to the understanding of the spatial and temporal aspects of the Hungarian tribes' migration. In the past few years, a great amount of archaic DNA-samples were collected as a first step of a research project that evaluates archaeological data with the help of bioarchaeological methods. The sampling area was extended from the Carpathian Basin to the Ural Mountains, to those regions that show the closest relations with the traces of the Hungarian migration as it is presumed on the basis of the increasing archaeological assemblages as well as traditional historical data. Our study offers a brief summary of the research of maternal lineages of populations lived in the Ural Mountains and the Volga-Kama region. The collection of the DNA-samples from the area expanding from the Carpathians to Western Siberia, was established with the help of Russian, Ukrainian and

Moldavian archaeologists and anthropologists. Due to the possibility of later publication in scientific journals, the data are presented here on the level of haplogroups, while our analyses are based on the complete mitochondrial DNA (mtDNA) sequences.

Between 2005 and 2010, following the international trends, Hungarian research has created a database depicting the genetic pattern of maternal lineage of the conquering Hungarians. This database not only has broadened since, but due to the spread of whole genome techniques it also has been renewed and rearranged in technological terms. Our current data are based on the so-called whole genome sequencing techniques and evaluation, which method helps to understand the relationship between populations and individuals in a more profound and - regarding the historical context - solid way. Since the conquering Hungarians appeared in the Carpathian Basin only in the 9th century, part of their population history has to be sought along the migration routes of the Hungarian tribes from east to the west. The exploration of these migration routes required research methods based mostly on archaeological artifact typology and traditional historical source analysis, even though

there is more and more legitimate criticism of these traditional methods, the use of which can be particularly problematic in the research of steppe areas. We tried to avoid the mere ethnical interpretation of archaeological cultures, and aimed to apply methodology often employed in similar researches of Indo-European populations. Due to the wide diversity of research and collection conditions within the sampling area, the variety in the amount of burials available in different territories, and also the various preservation statuses of the samples, our research team works with a sampling strategy that is based on archaeological data and accompanied with complex bioarchaeological approach. We collected samples from those cemeteries that revealed connections to the archaeological material of the 10th century Carpathian Basin. In addition, sampling was carried out in populations, presumably one-time neighbours (cemeteries and burials identified as Slavic, Alanic, Khazar or Bolgar) whose genetic compositions - according to historical evidences - are different from our genetic database. In this way, our sampling covers the entire territory of Hungarian ethnogenesis and its stages outlined on the basis of historical, linguistic and archaeological data. Currently, our database contains samples from 250 burials. Russian, Ukrainian and Moldovan archaeologists and anthropologists are also involved into the assessment of maternal lineages of the populations that is carried out along different schedules region by region. (Fig. 1.)

Besides samples suitable for DNA sequencing, we collected samples for radiocarbon dating as well. This not only provides the most accurate dating of the genetically characterized burials or cemeteries, but it also helps to interpret the results obtained by phylogenetic methods.

Our paper serves as a first step of a multi-stage work, and presents the primary results of the bioarchaeological research in the Cis-Ural and Trans-Ural regions. Accordingly, the most important criteria of the sampling were to collect samples from competently excavated and well documented cemeteries that show connections and similarities with archaeological material of the conquering Hungarians. Any samples with uncertain provenance were left out of the sampling procedure and we preferred to have series of samples instead of samples from individual burials taken out of their context.

Archaeological background

According to the current mainstream historical research, the Hungarian language developed in the Trans-Ural region between

1000 and 500 BC, and ancient Hungarians first moved to the Cis-Ural region in the 6th century AD. For some unknown reason, part of the population crossed the River Volga and settled in the Dnieper-Dniester region in the 8th century AD (based on linguistic arguments) or even in the first half of the 9th century (based on written sources and archeological data). They lived there during the second half of the 9th century until the Hungarian Conquest of the Carpathian Basin in 895 (Subbotsy archaeological horizon) (Иванов В. А. 1999; Комар 2011; Türk 2012).

Although the material culture of the 10th century Carpathian Basin changed rapidly, it reveals well-demonstrated archaeological connections with the assemblages of the above discussed Eastern European regions. This also served as a theoretical basis for the sampling procedure of our research. The Volga-Ural region played an important role in the early medieval (6th–10th century AD) history of Eastern Europe because the history of its peoples originated there and also because numerous population movements took place in the region that shaped the history of Europe as well. Instead of sporadic burials there are cemeteries with hundreds of graves suitable for analysis in this territory north of the steppe region, consequently the amount of archaeological data has increased explosively over the last 10–20 years. This meant a crucial aspect in the selection of our topic in this paper that is devoted to the bioarchaeological comparison of the Carpathian Basin and the Volga-Ural region in the early medieval period, with the following regions and cemeteries involved in the investigations.

Brief summary of the sites and archaeological cultures discussed in the archaeogenetic study

Uyelgi cemetery (Trans-Ural region)

The first among the investigated archaeological sites was the survey of the Uyelgi cemetery situated on the eastern side of the Ural Mountains and dated from the end of the 8th century until the beginning of the 11th century. The excavation of the late Kushnarenkovo culture site is still ongoing. Sampling was carried out in the previously discovered 10th century area of the cemetery and also in the 9th century section of the site that has been explored in 2015. The earliest artifact horizon of the cemetery appeared in the kurgans no. 10 and no. 32. On the basis of typochronological analysis, the finds of this horizon can be dated to the 9th century: flat, smooth surfaced silver mounts sometimes with ribs or hemisphere-shaped decoration. A very

archaic archery equipment typical of the 7th–8th centuries was unearthed as well, which refers to the oldest time horizon of the cemetery that can be dated to the turn of the 8th–9th centuries. This assumption is strengthened by the radiocarbon analysis, as it resulted in the period between 770 and 900 AD (with 95,4% probability). The younger part of the cemetery is located on a northern elevation in the northern area of the site. Graves of the 10–11th centuries can be distinguished from the 9th century burials on the basis of the typo-chronological differences of their metal finds: the appearance of plant ornament, gilt background and developed variants of double crescent-shaped mounts, although this issue still requires further research. The child's grave no. 7 of the kurgan no. 9 included finds both from the 9th and the 10th century. The grave no. 5 from the kurgan no. 7 can be dated to the 10–11th centuries according to the typo-chronological and radiocarbon analyses (1040±50 and 1053±50) as well (Грудочко and Боталов 2013).

Nevolino culture in the Cis-Ural Region

The Nevolino culture was located in the Kama-Valley at the western foothills of the Ural Mountains and represents the most significant and well-researched culture of the 4th–9th centuries history of the region. Its end was previously associated with the migration of Hungarians, therefore we investigated samples from all of its three chronological phases in accordance with archaeological chronology. The Brody cemetery can be dated to the 4th–5th centuries AD, the Bartym cemetery to the 6th–7th centuries AD, and Sukhoy Log cemetery after which the late phase of the culture has been named, is dated to the 8th–9th centuries AD. The Nevolino culture occupied about 15,000 sq. km in the southern zone of the forest area. As a result of long-distance trade activity of the population, there are clear archaeological connections with the east of the Urals, the Sasanian Iran, Byzantium, Central Asia and the Baltic Sea Region. The center of its research operates at the Department of Archaeology of the Udmurt State University in Izhevsk (Goldina and Chernykh 2005), (Голдина 2012), (Goldina, Pastushenko, and Chernykh 2013).

The Bayanovo cemetery in the Cis-Ural Region and the Lomovatovo culture

The Lomovatovo culture was situated in the western outskirts of the Urals, northeast of the area of the Nevolino culture in the Kama Valley, and can be dated to the 8th–10th century

AD. The Bayanovo cemetery is not only the most significant site of the culture, but due to its rich archaeological heritage, it also the most important archaeological site of the western territory of the Urals. Although the site has been discovered already in 1951, its intensive research began in 2005 under the guidance of the Department of History at the Perm State Humanitarian-Pedagogical University. The cemetery is dated to the 9th – beginning of the 10th century as it is proven by the radiocarbon analysis as well (Данич 2008).

The Novinki archaeological horizon

The kurgan cemetery of Novinki lay along the middle course of the Volga river, where the river crooks like an elbow in the area of Samara. In 1980, the archaeologist from Samara, Galina I. Matveyeva started to examine the archaeological material of the Khazar Khaghanate and Dmitry A. Stashenkov joined to the research in 1992. The archaeological assemblages from the second half of the 7th – 8th centuries represent the oldest remains of the early Bulgar population appeared in the Volga region. Besides their cemeteries, settlements are also known from the southern part of the Volga crook in Samara, which region offers a strategically suitable area for controlling the crossing of the Volga river (Матвеева Г. И. 1997).

Bolshie Tigani

The Bolshie Tigani cemetery in Tatarstan is one of the most famous sites connected with the ancient history of Hungarians. The early medieval cemetery lies on the left bank of the Santala river running near the Kama river. It was unearthed between 1974 and 1984 by the Tatar archaeologist, A. H. Halikov and his wife Ye. A. Halikova, and 156 graves were discovered during the excavations. The 10th century part of the cemetery was investigated in the 1980's, the first 56 burials of the cemetery's early phase have been published in Budapest in 1981 by the archaeologists of the Kazan Federal University. The recognition of the site significantly changed and advanced the archaeological research of early Hungarians. Most researchers now believe that the cemetery started to be used in the second half of the 9th century, thus the site is likely connected to the Hungarians stayed in the east, not to those who migrated to the west. Although Bolshie Tigani is classified as a site of the Kushnarenkovo-Karayakupovo culture, its different geographical situation together with its material characteristic of the Volga Bulgars distinguish Bolshie Tigani from the typical Bashkir sites of the Kushnarenkovo culture. The

partial horse burials, specific sabres, belt mounts and jewelry as well as the use of death masks and shrouds that are burial habits with Uralic origin, all represent connections with the heritage of the Hungarian Conquest Period (Chalikova and Chalikov 1981).

Chiyalikskaya Culture

The Chiyalikskaya culture dated back to the 10th–13th centuries has been determined in the southern part of Tartarstan by E. P. Kazakov. In our research, the material of Gulyukovo cemetery of the culture was investigated. Due to the local Islamization process, the amount of grave goods decreased significantly during the 12th–14th centuries. The cemetery shows connections with the supposedly Ugric, semi-nomad population of the Ural area, therefore majority of the archaeologists in the region identify this material as the heritage of the Hungarians who stayed in the east and had later been found by Friar Julian in the 13th century. This assumption can be reinforced by the presence of kurgan burials, shrouds placed on the eyes and mouths, handmade pottery with stamped decoration and the sporadic remains of partial horse burials. This material appears in the Trans-Ural region as well (Гарустович 1988).

Methods

During the initially sample collection we chose teeth and pieces of long bones. In the latter cases we examined petrous bone fragments. The majority of sampling was done by our team, during that we adapted our methods to the features and preservation of certain osteological collections in order to choose the best available samples, and avoid cross-sample contamination during the sampling.

Investigation of the ancient DNA, laboratory work

The ancient DNA requires sterile laboratory conditions, which was provided by the Laboratory of Archaeogenetics in the Institute of Archaeology, Research Centre for the Humanities, Hungarian Academy of Sciences. The work was done in sterile overall, overshoes, face-mask, face shield and gloves. The processes of the work took place in separate laboratory rooms. For the sterility all surfaces and tools were cleaned with DNA-ExitusPlus™ (AppliChem) and/or sodium-hypochlorite and irradiated with UV-C light. The archaic samples were processed in all workflows along with DNA free blank controls (in order to detect exogenous contamination). The mitochondrial DNA (mtDNA) haplotype of the laboratory staff was

also identified in order to percept recent DNA contamination.

In most of the cases we examined petrous bone fragments. This bone wasn't available from 10 individuals, who we analysed using teeth and long bone fragments.

We cut the samples out from the skulls or bones. Then we cleaned the samples' surfaces with sandblasting and sterilize the samples with UV-C light. Bone and tooth pieces were mechanically ground into fine powder in a mixer mill. Then we extracted DNA from bone powder (Dabney et al. 2013) (Lipson et al. 2017). The success of DNA extraction was verified by PCR reaction, which amplified fragments of the mtDNA (Szecsenyi-Nagy et al. 2015).

The next generation sequencing (NGS) requires DNA libraries that were prepared using UDG (uracil-DNA-glycosylase)-half treatment (Rohland et al. 2015), except for the samples from Gulyukovo. Hybridisation method was used to capture the target mitochondrial DNA fragments from the DNA libraries (Haak et al. 2015) (Lipson et al. 2017). This allowed the determination of the whole mitochondrial genome sequence in good quality. We got additional information about the samples (eg. genetic sex, endogenous DNA content) by random (shotgun) sequencing. Sequencing was performed on an Illumina MiSeq platform using the Illumina MiSeq Reagent Kit v3 (150-cycles) (Meyer and Kircher 2010).

Bioinformatics methods

Custom bioinformatics pipeline was created to process NGS data. The mapping was performed by BWA (Li and Durbin 2010), and various softwares were utilized for up and downstream analyses (Csáky et al. 2018).

The consensus sequences were created using the Geneious 8.1.7 (<https://www.geneious.com>) with minimum 3x coverage. Based on the mutational points, the haplogroups of the samples were determined by HaploGrep (v2.1.1) (<https://haplogrep.uibk.ac.at/>) on the basis of the conventional mitochondrial tree (phylotree.org) (van Oven and Kayser 2009).

Population genetic analyses

We compared statistically the analysed medieval populations with other archaic and recent populations available in international databases like NCBI GenBank. We used these data in the analysis of haplogroup frequencies (PCA - Principal Component Analysis and Ward cluster) and sequence-based statistics (MDS-Multidimensional scaling).

In the PCA and Ward cluster analyses, we compared the examined 4 populations

(RUS_Uyelgi (=site Uyelgi), RUS_W-Ural (=sites Bayanovo, Suhoy Log, Bartim, Brody), RUS-BTI (= site Bolshie Tigani), RUS-GUL (=site Gulyukovo)) with other 35 ancient and 64 modern populations. For hierarchical clustering we used Ward algorithm (Ward 1963) and Euclidean distance measurement.

When we calculated the pairwise genetic distances (FST) between populations, we compared the tested 4 populations with 19 ancient and 43 modern populations with Arlequin software v. 3.5.2.2 (Excoffier and Lischer 2010). We used Slatkin FST results for the MDS plots.

Phylogenetic analyses

Phylogenetic analyses are based on unique mtDNA sequences of the samples. With this method we can shed light on maternal relationships within and between the populations. Phylip software version 3.696 (Felsenstein 1989) was used to calculate the phylogenetic trees one-by-one for the observed haplogroups using neighbour-joining method.

Results

In our present study we investigated archaeological sites, cemeteries from the east (Uyelgi) and the west side of the Ural Mountains and the Kama valley (Bartim, Brody, Suhoy Log, and Bayanovo), from Bolshie Tigani and Gulyukovo cemeteries which represents the Chiyalikskaya culture and from Novinki habitat (from the Samara Bend of the Volga river) The samples from Bayanovo, Suhoy Log, Bartim, Brody represent Nevolino and Lomovatovo cultures. Although there is large chronological difference between these cemeteries (6th–10th AD), we regarded them as one group (West-Ural), due to their relative geographical proximity and related archeological interpretation, which connects them to the Hungarian prehistoric period based on archaeological and historical evidence.

At the current stage of our research we have 69 samples successfully sequenced and haplotyped, which came from Uyelgi site (20), West-Ural group (14), Bolshie Tigani (17), Gulyukovo (13) and Novinki (5) sites.

The distribution of genetic sex in the examined populations is shown in Fig. 2. The morphological sex, based on anthropological features, is confirmed by the genetic analyses. The sex distribution of the analysed samples does not reflect any cultural or biological condition, but only our consecutive sampling strategy, where we preferred anthropologically male remains bearing in mind the plans of subsequent Y chromosomal analyses.

The mtDNA haplogroup composition of the examined groups are illustrated in Fig. 3. The haplogroup compositions are heterogeneous, both European and Asian maternal components are observed in different rates within and between populations.

The samples from Novinki site don't show parallels with the archaeological heritage of the early Hungarians. The selection of the site is not based on archaeological data but on the assumption that its population was neighbours of ancient Hungarians. Owing to the low number of samples (5) from Novinki site, we excluded them from further statistical analyses.

We compared the studied groups (RUS_Uyelgi, RUS_W-Ural, RUS_BTI, RUS_GUL) to ancient and modern populations in the haplogroup frequency based PCA analysis. The PCA separated spectacularly the Asian and European archaic populations on the X axis, where our groups are placed in an intermediate position (Fig. 4). In this plot the studied groups are situated closest to the Altaian Scythians (ALT_Scythians), to the South-Central-Siberian Bronze Age population (Min_BRAge), to the Hungarian Conquerors from the Carpathian Basin (Hun_Conq) and to the Andronovo culture's population from Siberia (SIB_Andronovo).

In all performed statistical tests, the Gulyukovo and Uyelgi populations are the closest to each other. In these analyses the West-Ural group is far from the other three investigated populations. This phenomenon can be at least partially attested to the relative small sample size of the merged group and the relative high frequency of U haplogroups.

The PCA plot with recent populations also represents an East-West Eurasian cline, and while the position of our groups remains approximately intermediate, the closest relatives appeared to be Central Asian, South Asian, Turkmenian and Uzbek populations (plot is not shown).

The Ward clustering is based on the haplogroup frequency as well. This analysis shows a close Uyelgi – Gulyukovo and a West Ural – Bolshie Tigani relationship, placed them together into the same subcluster, but separated by three branches (Fig. 5).

We performed the Ward analysis with modern populations as well. The results almost perfectly mirror the relationships between the ancient groups, as seen in Fig. 5. One subcluster of the dendrogram comprises modern Khanti, Mansi, Turkmenian, Uzbek, Central Asian Pathan and Burusho populations together with the four studied ancient populations (Ward

plot is not shown). These results indicate that the clustering of the ancient populations is independent from the characteristics of the comparative dataset.

The FST calculation is a sequence based analysis, which serve as a basis for multidimensional scaling (MDS) and plotting, used to visualize the genetic connections of the analysed groups. The distribution of the ancient populations on the MDS plot highly resembles the PCA plot. Uyelgi and Gulyukovo populations form an eastern group with the Avar periode elite of the Carpathian Basin, the Thian Shan Central-Asian medieval (C-Asia_Medieval) and the Central-Asian Late Iron Age and Hun period (C-Asia_LIAge) populations. Bolshie Tigani and the Iron Age nomads from Central-Asia are close to each other, between the European and the Asian clusters. The West-Ural, the Russian Bronze Age (RUS_BRAGE), the Hungarian Conquerors (HUN_Conq) and the Eastern-European Scythians from today's Ukraine and Moldova (E-EU_Scythians) form another set, more attached to a cluster composed of mostly European populations (Fig.6).

The studied groups compared to modern populations in the MDS analysis are close to populations of modern Central and South Asia. The modern Hungarians however show connections to modern Central European populations.

Utilizing whole mitochondrial sequences and available GenBank datasets, we were able to create phylogenetic trees of subhaplogroups and shed light on close maternal relationships of each newly analysed individual. Each subhaplogroup has its own phylogeography (geographical distribution of maternal lineages) and history, thus we could trace back the origin of several maternal lines, and define the closest known relatives of a certain individual. Some peculiar subhaplogroups (independent of its geographical origin) has shown close and direct relations between and within the studied populations and the Hungarian Conquerors. A good example for such relations is the phylogenetic tree of T2d1b1 subhaplogroup shown in Fig. 7, where mitochondrial sequences of two individuals from Gulyukovo and two from Bolshie Tigani turned out to be identical, and situated within a Siberian cluster on the tree. This indicates common source of maternal ancestry, but it could even represent a direct family level kinship between the two populations. Same or similar connections can be observed frequently among the detected maternal lineages.

Conclusion

In this study, the populations from four regions under investigation show archaeological connections to the heritage of the early Hungarians. Each represents a highly heterogeneous mitogenome diversity, consisting of a wide range of Eurasian maternal lineages. Our statistical analyses support their intermedial position between classical European and Asian populations. Strong and direct within and between population connections are visible at the individual level in this study, which is also conspicuous comparing them to the Hungarian Conquerors. This observation supports our previous hypothesis (Csősz, et al. 2016.) about the origins of the Hungarian Conquerors, whose mitogenomic diversity was highly influenced by 6th–10th AD ancient populations of the Volga-Ural region. Besides, other maternal genetic connections between populations of the archaeological cultures of the Cis- and Trans-Ural region can be observed, but these seem to be independent from the Hungarian Conquerors themselves. These connections are probably mirroring the geographical proximities and genetic continuity of populations of archaeological and/or chronological horizons. To provide more precise conclusions and descriptions about this phenomenon, the sampling range shall be extended to populations that were independent of the archaeology of the early Hungarian history.

Further plans

To obtain a more comprehensive view of the early history of Hungarians, origins and migration routes with genetic analyses, we would like to involve an elevated number of sites that can be associated with ancient Hungarians or theirs ethnogenesis. It is also important to include samples unassociated to archaeological evidence of the early Hungarian history as a controll to refine the picture of past migration events. Furthermore, we would like to utilize the Y chromosome for inferring paternal lineages, and comparing them to maternal ones in context of kinship, migration, inheritance and origins. We also aim to analyse autosomal variations, which nowadays plays a crucial role in population genetic studies.

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РЕЗУЛЬТАТЫ ПАЛЕОГЕНЕТИЧЕСКИХ ИССЛЕДОВАНИЙ МАТЕРИНСКОЙ ЛИНИИ ДНК РАННЕСРЕДНЕВЕКОВЫХ ПОПУЛЯЦИЙ (VI–X ВВ. Н.Э) ЗАУРАЛЬЯ, ПРИУРАЛЬЯ И ВОЛГО-КАМЬЯ В СВЯЗИ С ПРОБЛЕМОЙ ВЕНГЕРСКОГО ЭТНОГЕНЕЗА

**Беа Сейферт, Вероника Чакева, Балаж Стегмар, Даниэл Гербер, Балаж Эгнел,
С.Г. Боталов, Р.Д. Голдина, Аттила Тюрк, Балаж Густав Менде,
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О происхождении ранних мадьяр, об их миграции из Северо-Центральной Азии существует несколько научных теорий. Пестрый этнический состав венгров эпохи обретения родины доказан археологическими и историческими источниками. Когда они пришли в Карпатский бассейн через восточноевропейскую степь и территорию Хазарского Каганата, в их составе были разные народы. Исходная территория, направление, хронология миграции мадьяр до сих пор считаются спорными вопросами среди историков, лингвистов, археологов. Наши исследования раскрывают археогенетический аспект этой проблематики. Мы изучаем раннесредневековые (VI – X вв.) популяции в Карпатском бассейне на Урале и на тех территориях, которые, возможно, связаны с миграцией мадьяр. Данные территории связаны друг с другом схожим археологическим материалом. Население кушнаренковской и караякуповской культур отождествляется с мадьярами, их первые памятники появились на Среднем и Южном Урале. В наших исследованиях мы изучали образцы с восточной (Уелги) и западной (Бояново, Бартым, Сухой Лог) сторон Среднего Урала, их полную митохондриальную ДНК. Продолжая эти исследования, мы рассмотрели Волжско-Камский регион, особенно материалы Больше-Тиганского могильника. Данные митохондриальных ДНК этого памятника позволяют обновить нашу базу данных, используя которую мы можем получить более точную картину о пути миграции мадьяр в контексте генетики.

Ключевые слова: Митохондриальная ДНК (мтДНК), материнская линия, популяционная генетика, праистория древних венгров, Приуралье, Зауралье, Волжско-Камский регион.

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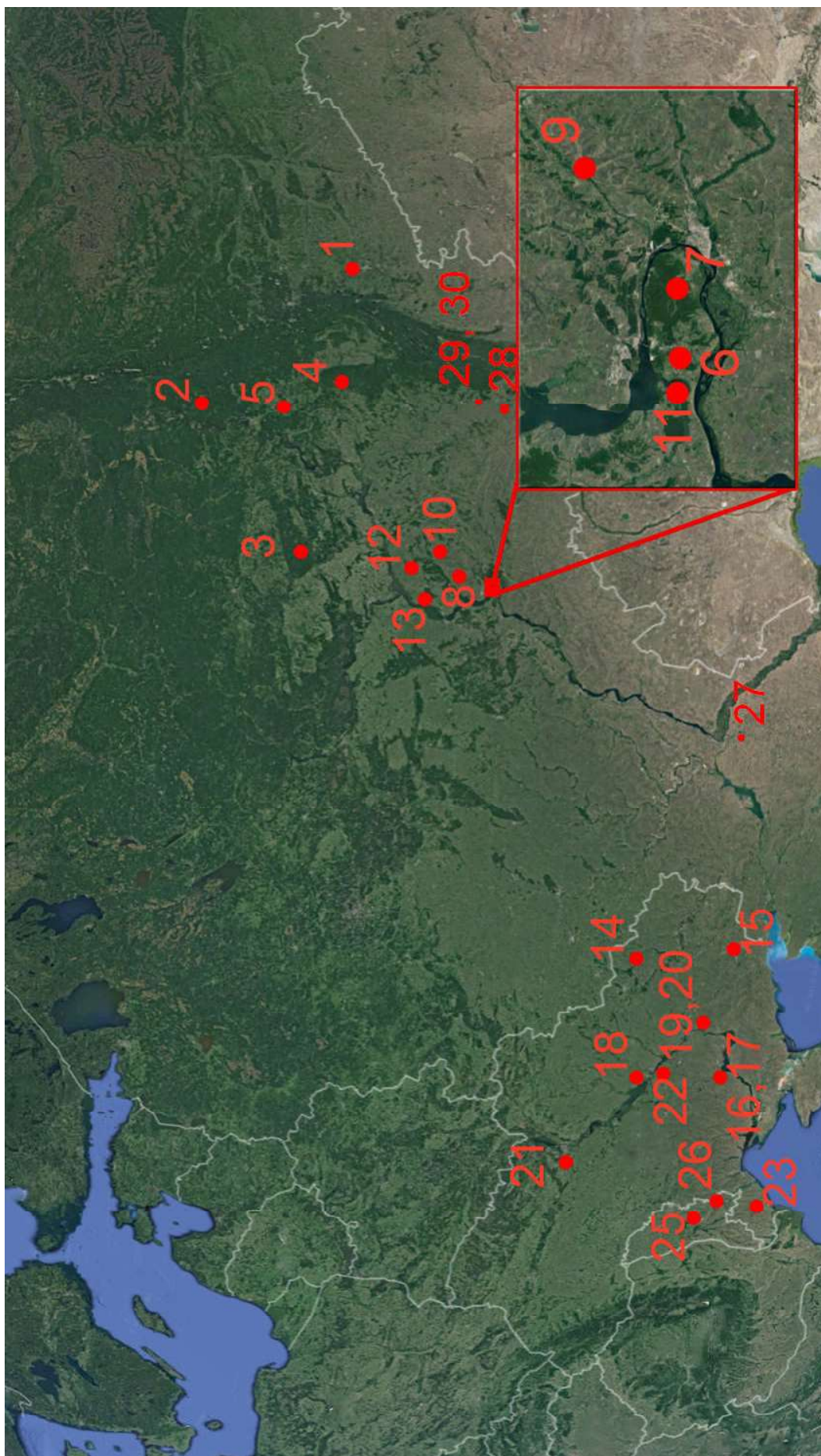


Fig. 1. The origin of the collected samples that have archaeological connections with the history of the early Hungarians.

1 – Uyelgi, 2 – Bayanovo, 3 – Suhoy Log, 4 – Bartim, 5 – Brody, 6 – Brusyany, 7 – Novinki, 8 – Mullovka, 9 – Lebyazhinka, 10 – Shilovka, 11 – Malaya Ryazan, 12 – Bolshie Tigan, 13 – Tankeyevka, 14 – Verhniy Saltov, 15 – Krasnaya Gorka, 16 – Katerinovka, 17 – Novovorontsovka, 18 – Dmitrovka, 19 – Kamennoe, 20 – Zeleny Gaj, 21 – Kazarovichi, 22 – Vinogradovka, 23 – Trapovka, 24 – Zhovtneve, 25 – Kisinov (Sadovo, Alcedar), 26 – Tiraspol (Slobodzeya, Glinoje), 27 – Sokolovskaya Balka, 28 – Karanaevo, 29 – Gornovo, 30 – Gulyukovo

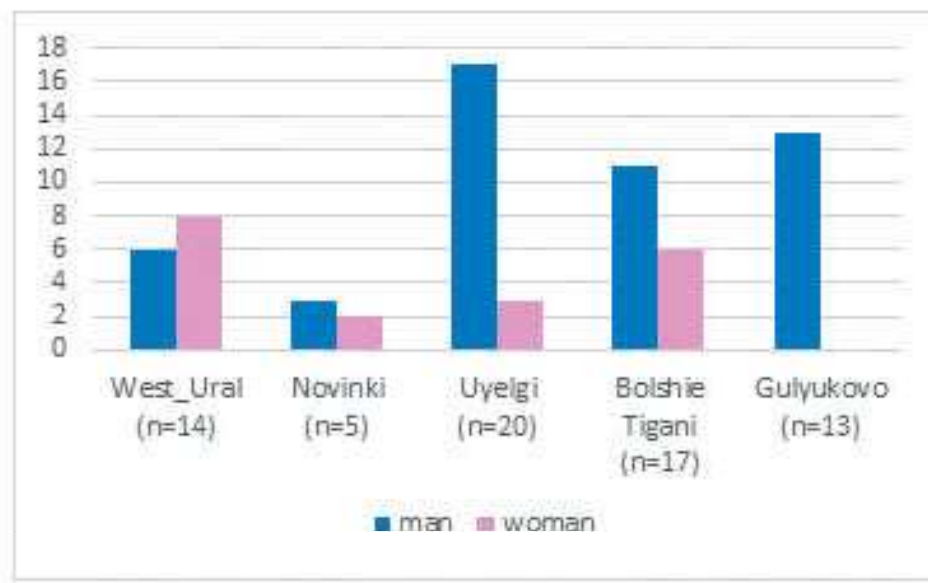


Fig.2. The number of males and females in the examined populations. Determined by genetic methods.

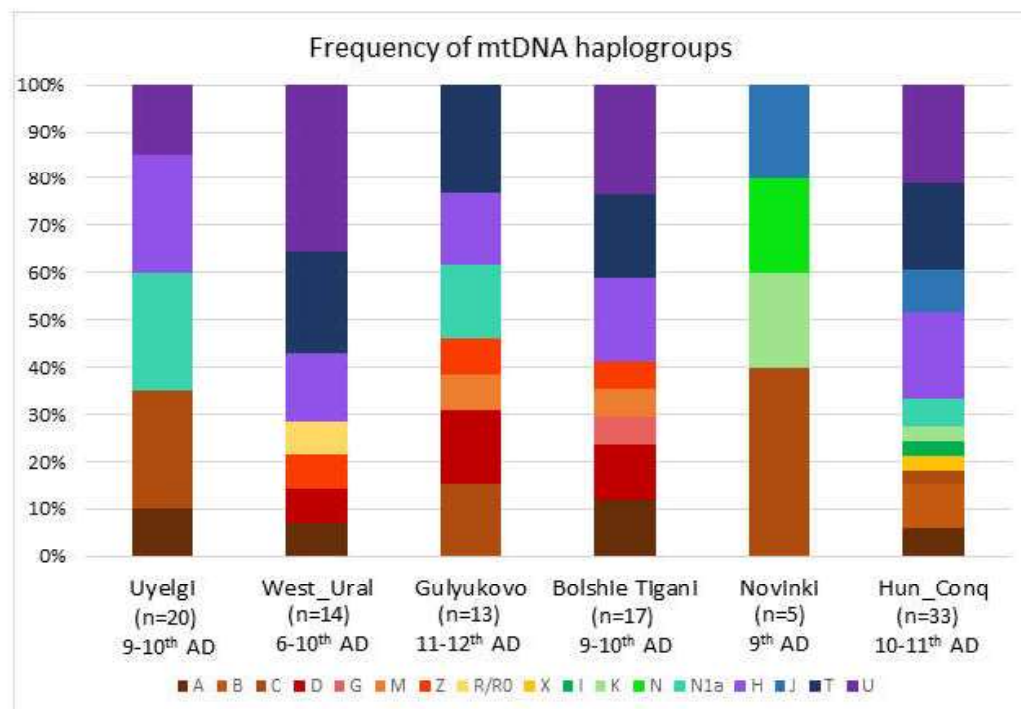


Fig. 3. The haplogroup composition of the examined populations (and the Hungarian Conqueror population). We indicated the population from East to West (migration's supposed route). The red / brown / yellow colors are show the East Eurasian, blue / purple colors are show the Western Eurasian haplogroups. Eight samples in the Hun_Conqueror population (Hungarian Conquerors from the 10th century Carpathian Basin) came from our own unpublished research, whereas 25 samples came from Neparáczky et al. (Neparáczky et al. 2017)

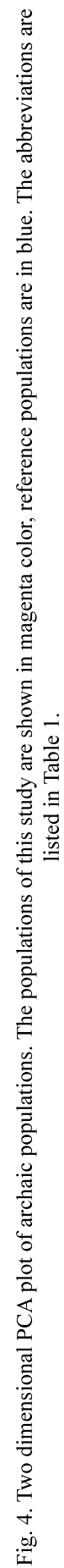
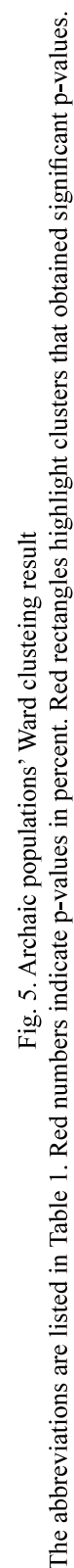


Fig. 4. Two dimensional PCA plot of archaic populations. The populations of this study are shown in magenta color, reference populations are in blue. The abbreviations are listed in Table 1.



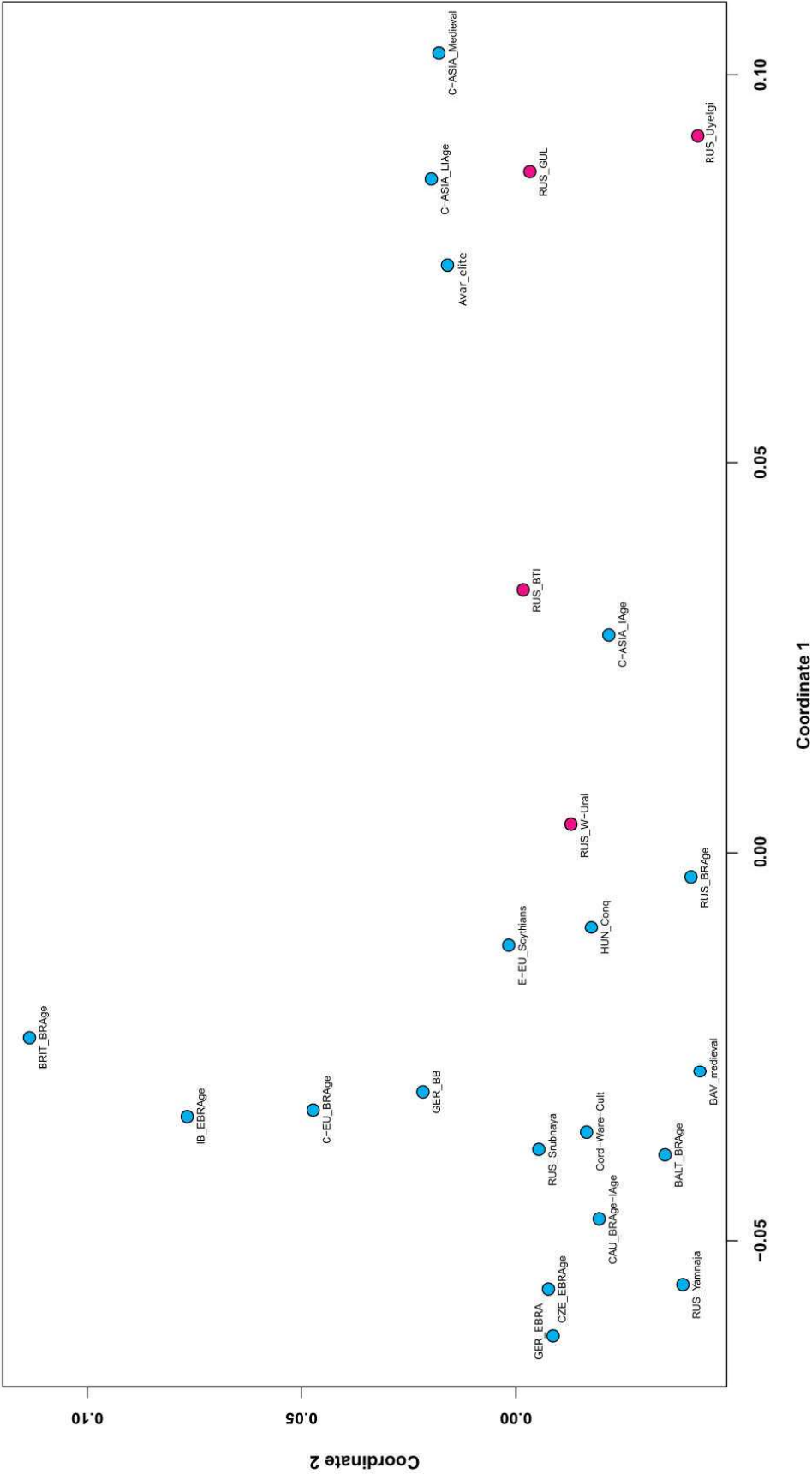


Fig. 6. MDS plot of the archaic populations The studied populations are shown in magenta color. The abbreviations are listed in Table 1.

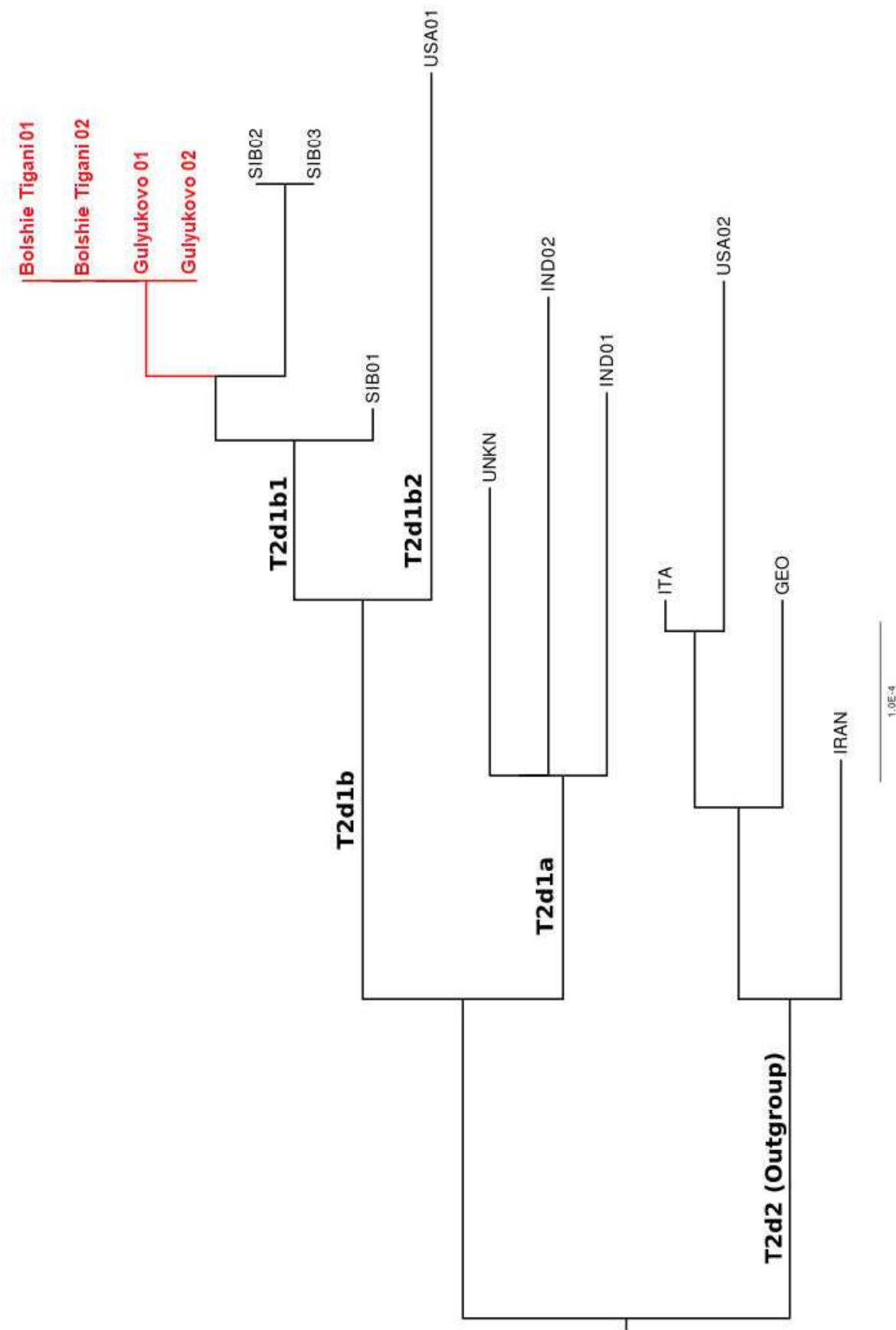


Fig. 7: Phylogenetic-tree of the haplogroup T2d1, using neighbour-joining method. Samples from our own research were marked in red. Red-colored samples are identical at the sequence level, implying close maternal relationship between them.

Table 1.
Abbreviations of archaic populations

Ancient populations				
Abbreviation	Population	Region, Country	Century	Reference
1. RUS_Uyelgi	Uyelgi	Russia	9 th - 10 th AD	This study
2. RUS_W-Ural	Bayanovo, Suhoy Log, Bartim, Brody	Russia	7 th - 10 th AD	This study
3. RUS_BTI	Bolshie Tigani	Russia	7 th - 10 th AD	This study
4. RUS_GUL	Gulyukovo	Russia	11 th -12 th AD	This study
5. ALT_Scythians	Scytho-Siberian	Altai Republic, Mongolia	5 th -3 rd BC	(Ricaut et al. 2004) (González-Ruiz et al. 2012) (Allentoft et al. 2015) (Pilipenko et al. 2010)
6. AVAR	Avar period (catacomb graves group)	Hungary	6 th –8 th AD	(Csósz et al. 2016)
7. AVAR-elite	Avar period elite	Hungary	7 th AD	(Csáky et al. 2018)
8. BALT_BRAge	Balthic Bronze Age	Latvia, Lithuania	2100/2000-230 BC	(Mittnik et al. 2018)
9. BAV_medieval	Early medieval burials from Bavaria	Germany	5 th -7 th AD	(Veeramah et al. 2018)
10. BRIT_BRAge	Great Britain Bronze Age	England, Scotland, Wales	2500-1010 BC	(Olalde et al. 2018)
11. C-Asia_IAge	Central Saka, Tian Shan Saka, Sarmatian, Iron Age nomads,	Central Steppe, Thian shan, Caspian steppe	8 th –1 st BCE	(Damgaard et al. 2018)

Ancient populations				
Abbreviation	Population	Region, Country	Century	Reference
12. C-Asia_LIAge	Hun-period Nomads, Hun-Sarmatians and Huns from Tian Shan	Central Steppe, Thian shan	4 th –5 th BCE	(Damgaard et al. 2018)
13. C-Asia_Medieval	Turks from Central Steppe and Tian Shan, Karluk, Kipchak, Kimak, Karakhanid Golden Horde and medieval nomads	Central Steppe, Thian shan, Caspian steppe	5 th –13 th AD	(Damgaard et al. 2018)
14. CAU_BRAGE-lage	Caucasian Bronze Age-Iron age	Armenia	3500–500 BC	(Margaryan et al. 2017) (Allentoft et al. 2015)
15. CB_cont-zones	medieval populations from present-day Slovakia	Slovakia, Croatia	10 th –11 th AD	(Csákyová et al. 2016) (Csősz et al. 2016)
16. C-EU_BRAGE	Central Europe Bronze Age	Hungary, Poland	2900–1800 BC	(Olalde et al. 2018) (Allentoft et al. 2015) (Gamba et al. 2014)
17. CHIN_Xianbei	Tuoba Xianbei	China-Inner Mongolia	4 th –5 th AD	(Changchun et al. 2006)
18. CHIN_WANG-ZHEN	Wanggu, Upper Capital - Zhenzishan	China-Inner Mongolia	12 th –14 th AD	(Fu et al. 2007) (Fu et al. 2009)
19. CZE_EBRAGE	Czech Early Bronze Age	Czech Republic	2500–1700 BC	(Olalde et al. 2018) (Allentoft et al. 2015)
20. Cord-Ware-Cult	Cord Ware Culture	Germany, Estonia, Poland, Czech Republic	2900–2050 BC	(Haak et al. 2015) (Olalde et al. 2018) (Mathieson et al. 2015) (Allentoft et al. 2015) (Brotherton et al. 2013)
21. DAN_Vikings, medieval	medieval Danes and Vikings	Denmark	8 th –16 th AD	(Melchior et al. 2010)
22. E-EU_Scythians	East Europe Scythians	Ukraine, Moldova	7 th –2 nd AD	(Juras et al. 2017)

Table 1.
Abbreviations of archaic populations

Ancient populations					
Abbreviation	Population	Region, Country	Century	Reference	
23. GER_Bell-Beaker	Bell Beaker	Germany	2500-2000 BC	(Knipper et al. 2017) (Haak et al. 2015) (Brotherton et al. 2013) (Olalde et al. 2018) (Mathieson et al. 2015) (Allentoft et al. 2015)	
24. GER_EBRage	Germany Early Bronze Age	Germany	2200-1500 BC	(Knipper et al. 2017) (Haak et al. 2015) (Brotherton et al. 2013)	
25. HUN_Conq	medieval populations of Conquest period from Hungary	Hungary	10 th - 12 th AD	(Csősz et al. 2016) (Neparáczi et al. 2017) (Tömöry et al. 2007)	
26. HUN_Lombards	Lombards from Hungary: Szóliád	Hungary	6 th AD	(Alt et al. 2014)	
27. IB_EBRage	Iberian Early Bronze Age	Spain, Portugal	3100-1700 BC	(Lipson et al. 2017) (Olalde et al. 2018) (Mathieson et al. 2015)	
28. ICE_medieval	early medieval Icelandic	Iceland	10 th - 12 th AD	(Helgason et al. 2009)	
29. ITA_Lombards	Lombards from Italy	Italy - Piedmont	6 th - 8 th AD	(Vai et al. 2015)	
30. ITA_medieval	medieval Italians	Italy - Tuscans	10 th - 15 th AD	(Guimaraes et al. 2009)	
31. KAZ_BRage-lage	Ak-Mustafa; Izmaylovka; Ozhaylau-III; Vodokhranilische; Zevakinskiy; Birlík; Molaly, Shubarat; Kok-Mardan; Solyanka; Bulanovo; Stepnoe VII; Bol'shekaraganskii; Kapova cave; Tanabergen II	Kazakhstan, Russia	23 rd - 4 th BC	(Lalueza-Fox et al. 2004) (Allentoft et al. 2015)	
32. MIN_BRage	Solenozernaia; Tatarika; Oust-Abakansty; Bogratsky; Afontova Gora, south central Siberia	Russia - Minusinsk Depression	18 th - 9 th BC	(Keyser-Tracqui et al. 2003) (Allentoft et al. 2015)	
33. MON_Xiongnu	Xiongnu period: Hsiung-nu	Mongolia	3 rd BC - 2 nd AD	(Keyser-Tracqui et al. 2003) (Kim et al. 2010)	

Ancient populations					
Abbreviation	Population	Region, Country	Century	Reference	
34. NOR_Viking	Vikings from Norway	Norway	6 th - 11 th AD	(Krzewinska et al. 2014)	
35. POL_medieval	medieval Slavs from Poland	Poland	11 th - 15 th AD	(Juras et al. 2017)	
36. RUS_BRAge	Russia Bronze Age	Russia	3000-1200 BC	(Mathieson et al. 2015) (Allentoft et al. 2015)	
37. RUS_Srubnaya	Srubnaya, Russia - Samara	Russia	2000-1200 BC	(Mathieson et al. 2015)	
38. RUS_Yakuts	Yakuts	Russia - Eastern Siberia	15 th - 19 th AD	(Crubézy et al. 2010)	
39. RUS_Yamnaja	Yamnaja-Samara, Kalmykia	Russia	3300-2100 BC	(Haak et al. 2015) (Allentoft et al. 2015)	
40. SVK_Avar-Slavic	Cífer-Pác, Avar-Slavic burial	Slovakia	8 th - 9 th AD	(Šebest et al. 2018)	
41. SIB_Krotovo	Early-Late Krotovo	Russia	23 rd - 17 th BC	(Molodin et al. 2012)	
42. SIB_Baraba	Baraba, Late Bronze Age	Russia	13 th - 7 th BC	(Molodin et al. 2012)	
43. SIB_Andronovo	Andronovo	Russia	20 th - 13 th BC	(Molodin et al. 2012) (Allentoft et al. 2015)	
44. SPA_medieval	medieval Spaniards: Basque, Aldaieta	Spain	6 th - 7 th AD	(Alzualde et al. 2006)	